Ecological Monographs, 61(1), 1991, pp. 33–51

DYNAMICS OF CANOPY STRUCTURE AND LIGHT INTERCEPTION IN *PINUS ELLIOTTII* STANDS, NORTH FLORIDA[1]

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Abstract. In order to develop a model of the carbon cycle for mature slash pine (*Pinus elliottii*) stands in north Florida, we studied seasonal variation in leaf area index (LAI, all-sided), aboveground biomass increment and litterfall, and light penetration through the forest canopy, over a 3-yr period. The primary approach to establishing monthly LAI included annual destructive analyses and monthly measurements of needle fall and elongation. Imagery from the Landsat Thematic Mapper (TM) and patterns of light penetration were also used in attempts to derive less arduous estimates; the TM imagery was most promising.

LAIs ranged from 3.0 to 6.5 on control plots over the 3 yr, with repeated fertilization increasing maximum LAI by >40%. Seasonal variation was high (40%), as was variation from year to year. An average of 31% of the incident photosynthetically active radiation (PAR) penetrated the canopies annually, ranging from 18 to 42% seasonally. Seasonal light penetration could not be described using a simple application of the Beer-Lambert law, perhaps due to the highly aggregated nature of the canopies. Models incorporating more information on canopy structure are necessary to predict light penetration through slash pine stands accurately.

A model of needle litterfall was derived that could account for much of the seasonal and annual variation using stand basal area and climate conditions from the spring of the previous year; this model may be useful for developing climate-driven predictions of LAI. Efficiencies of use of incoming and intercepted PAR were low compared to other forest types. Low light interception and high nutrient-use efficiencies (demonstrated in earlier studies) are important adaptive characteristics of slash pine stands to these relatively warm and nutrient-poor sites.

Key words: biomass; canopy structure; Florida; leaf area index (LAI); light interception; litterfall; needle elongation; photosynthetically active radiation (PAR); Pinus elliottii; *remote sensing; seasonal change; slash pine.*

INTRODUCTION

The need to estimate the structure and productivity of ecosystems is increasingly driven by the need to understand the impacts of such large-scale phenomena as land-use changes, regional pollution, and global climate change. Foliar biomass and leaf area index (LAI), for instance, are key measurements for understanding rates of material and energy exchanges between plant canopies and the atmosphere. However, such estimates are particularly difficult to obtain for forests, where access to the canopy is difficult and the foliage is distributed heterogeneously. Moreover, a common simplifying assumption for closed-canopy forest stands, that LAI is constant from year to year (Cole and Rapp 1981, Beadle et al. 1982, Gholz 1982, Waring 1983), has not been substantiated in most stands, and may be erroneous (McMurtrie et al. 1989, Vose and Swank 1989). Models that would assist in predicting responses to changes in environmental conditions and the physiological status of trees have been limited by our inability to simulate growth of individual cohorts of foliage mechanistically (Rook et al. 1985). Detailed models of canopy processes must therefore be restricted to relatively short intervals during which static leaf areas can be reasonably assumed (e.g., Grace et al. 1987*a*, Smolander et al. 1987).

In addition, the need to estimate structure and productivity on scales larger than single stands has become important in the development of regional and global models that will provide an understanding for larger implications of local management practices. Techniques that may be appropriate for these estimates are becoming available. Single measurements of relative

[1] Manuscript received 17 November 1989; revised 17 May 1990; accepted 8 June 1990; final version received 5 July 1990.

light absorption by forest canopies may be useful in estimating LAI (Ross 1981, Pierce and Running 1987). Remotely sensed radiation in near-infrared (NIR: 760–900 nm) and red (R: 630–690 nm) wavebands also has the potential for use in estimating LAI. In NIR wavelengths, within-leaf scattering is high and therefore reflection from the canopy is high, but in R wavelengths pigment absorption is high and therefore reflection is low (Curran 1983, Jensen 1983). Consequently, LAI is usually related positively to an increase in the difference between NIR and R (Ashcroft et al. 1990, Girard et al. 1990), at least up to the reflectance asymptote of the canopy. For both these techniques, however, basic stand-level information is critical for deriving and validating the relationship between remotely sensed data and LAI.

In order to develop a model that would demonstrate the interrelations among carbon, nutrients, and water in managed slash pine (*Pinus elliottii* var. *elliottii*) stands in Florida, we made seasonal estimates of canopy biomass and LAI (all-sided) for 3 yr. Because of the structural simplicity of our stands and the variability we were able to induce with fertilization, we were also able to investigate the validity of less time-consuming destructive techniques for measuring these parameters. We addressed several questions about seasonal and annual variability of canopy biomass and LAI, productivity rates that are derived from them, their effect on light penetration patterns, and the ability of remote-sensing techniques to predict them.

Our effort was directed first at determining whether foliar biomass and LAI of a closed-canopy stand are constant from year to year. We questioned how significant the magnitudes and timing of seasonal variations within a year might be, particularly with respect to calculations of annual exchanges of energy and material between the atmosphere and the canopy. We also investigated whether annual fluctuations might be predictable.

We were also interested in the hourly and daily patterns of light penetration through canopies of unfertilized and fertilized slash pine stands. We wanted first to test whether aboveground net primary production (ANPP) could be predicted from absorbed photosynthetically active radiation (PAR), as suggested for crops (Monteith 1972) and forests (Linder 1985, Sellers 1985, Grace et al. 1987*b*). We also wanted to use these data to evaluate the applicability of light-penetration models to slash pine canopies. Additional measurements of light penetration in our fertilized and unfertilized stands also enabled us to test the validity of a new instrument for estimating foliar biomass and LAI.

Finally, we estimated LAI from satellite sensor images taken during three times in 1988 and 1989. The data we had gathered in the projects above enabled us to validate this technique, which may allow estimates to be obtained over greater ranges of space and time.

Study Site

The study site was a 60-ha block of plantation slash pine in Alachua County, 20 km northeast of Gainesville, Florida (29°44′ N, 82°9′30″ W). The soil is sandy and characterized by low organic matter and nutrient status, with a water table that fluctuates between the surface and ≈2 m depth over a typical year. The predominant soil type is an Ultic Haplaquod, although the relative development of the diagnostic subsurface spodic (organic) and argillic (clay) horizons is highly variable over the study area (Gaston et al. 1990). The area is 39.5 ± 1.8 m ($\bar{X}$ ± SD) elevation, draining slowly into nearby wetlands. The mean annual (1955–1987) precipitation is 1342 mm and the mean annual temperature is 21.7°C (NOAA 1989). Rainfall totals for May 1987–April 1988 and May 1988–April 1989 were 1051 mm and 1125 mm, respectively.

The vegetation was dominated by even-aged planted pines that were 21 yr old in 1986 (Appendix 1), the first year of the study; slash pine is native to these sites. Site preparation after the stem-only harvest of the former plantation stands (the current stands are second rotation) consisted of chopping the residues, broadcast burning, bedding, and machine-planting new trees. After establishment there was no further treatment of the stands. The canopies of similar stands reach maximum LAI by ≈12 yr (Gholz and Fisher 1982), and we initially assumed that LAI of untreated stands would be constant from year to year (Tadaki 1963).

Understory vegetation consisted of native species reestablished naturally after site preparation, primarily *Serenoa repens* and *Ilex glabra*. Although detailed analyses of understory diversity and structure have been completed, we will confine our discussion in this paper to the tree stratum only.

In 1986 we established 16 plots within the study area. Each plot was 50 × 50 m, with vegetation measurements confined to an internal 25 × 25 m subplot. At least 100 m separated adjacent plots. Fertilizers (Appendix 2) were added quarterly beginning in February 1987 to eight plots, and eight other plots served as controls.

Methods

Canopy dynamics and ANPP

To establish patterns of seasonal foliar biomass, LAI, and their responses to altered fertility, we conducted intensive, annual destructive sampling and measured needlefall and needle-elongation patterns monthly. To develop a data set for testing light-penetration models we also measured the penetration of direct-beam radiation through the canopy, relative PAR above and below the canopy, and radiation reflected from the canopy to a satellite sensor.

To define foliage cohorts and to integrate our sampling into clearly defined year intervals, we selected

pre-bud-burst in early March as the anniversary date. Foliage emerging after that date each year was defined as "new," and foliage remaining on the tree prior to that date was defined as "old." We began the study in midsummer 1986 with two cohorts of foliage on the trees, and ended it in late summer 1989, again with two cohorts on the trees.

Destructive sampling.—Tree diameters at breast height (dbh, measured at 1.3 m) were inventoried on all measurement plots in July 1986, 1987, and 1988. Trees from the control and fertilized plots were pooled by treatment and separated into six dbh classes: ≤12.5 cm; >12.5–15.0 cm; >15.0–17.5 cm; >17.5–20.0 cm; >20.0–22.5 cm; and >22.5 cm. The number of trees sampled from each class was proportional to the number of trees in the class, with a total of 20 per treatment in 1986 and 1987, and 30 per treatment in 1988. The sampled trees were cut from the buffer areas of corresponding plots. We sampled each year to test the assumption that LAI is constant from year to year in closed-canopy stands. The larger number in 1988 reflected our hypothesis that this would be the first year in which a treatment effect would be manifest; if treatment differences were not significant, data could be pooled within-year.

Trees were cut between the last week in July and the first week in August each year. (For clarity we refer to these as August measurements.) In the field, stem lengths, crown lengths, and stem diameters at the base, base of the live crown, and middle of the live crown were measured using cloth tapes. In 1986 only, whole stems were weighed fresh in the field and subsampled to determine relative proportions of wood and bark and moisture contents in the laboratory. From these data relationships of stem or bark biomass to dbh were derived. Because fertilization increases slash pine stem biomass but does not significantly change these relationships (Jokela et al. 1989), we only sampled stems once, and applied the 1986 relationships for 1987 and 1988. The single equations for stem wood (SW) and bark (SB) biomass (in kilograms per tree) were:

$$\ln(\mathrm{SW}) = -3.9330 + 2.8800 \ln(\mathrm{dbh}) \qquad n = 40,\ R^2 = 0.91, \tag{1}$$

and

$$\ln(\mathrm{SB}) = -3.3170 + 2.0780 \ln(\mathrm{dbh}) \qquad n = 40,\ R^2 = 0.80. \tag{2}$$

Foliage was sampled in vertical 1-m segments of the crown of each tree from the top of the tree below the base of the leader. In each segment, live branches were divided into two size classes and numbered. Then one branch from each size class was selected randomly for the following measurements: primary branch length, diameter at the base, foliated length, diameter at the base of the live foliage, numbers of higher order branchlets, and numbers of clumps of foliage. Each branch was then separated into five components for dry mass (70°) determination: new (<1-yr-old) foliage, new foliated twig, old foliage, old foliated twig, and unfoliated branch. To reconstruct the biomass of the canopy, sample branch dimensions and dry masses from each 1-m segment were multiplied by the number of branches in the segment and summed over the tree.

We used the General Linear Model (GLM) procedure of the Statistical Analysis System (SAS) (Freund and Littell 1979) to analyze the individual tree data. The regression model used was:

$$Y_0 = a_0 + a_1(X) + a_2(I_{yr}) + a_3(X)(I_{yr}), \tag{3}$$

where Y_0 is the logarithm of tissue biomass; X is the logarithm of dbh; I_{yr} is a classification variable for the different years (0, 1, 2), a_0 is the intercept, and a_1 is the slope of the linear model. Using this model, if $a_2 = 0$ the relationships for 2 yr have the same intercepts; if $a_3 = 0$ the slopes are equal, and if $a_2 = a_3 = 0$ the relationships are identical. GLM provided tests for 1987–1986 and 1988–1986; a CONTRAST statement was used to generate the 1988–1987 comparison. Student's t tests were used to determine the significance of observed differences between coefficients. Effects of plot fertilization on regression models within a year were tested with a similar model, but using an I_F term (control plots = 0, fertilized plots = 1) instead of I_{yr}. Finally, equations were applied to each year's dbh inventory to calculate the August biomass for each year and tissue.

Tree growth and ANPP.—Whole-tree mortality was negligible in all plots during this study; only four small suppressed trees were lost between 1986 and 1989 from the control plots and three from the fertilized plots. Therefore, to determine annual tree dbh changes, and hence growth, we extracted increment cores from a sample of trees in September 1989 (at the end of the final growing season). One core each from 10 trees per plot was extracted, with the trees selected proportional to their frequency in the dbh classes as established above (see *Destructive sampling*). Radial growth for each year was measured on the cores under 10× magnification to the nearest 0.1 mm. Annual changes in dbh from 1980 through 1989 were then calculated using the 1987 dbh inventory as the baseline. We felt that this procedure was superior to relying on the annual dbh surveys for precise measurements of dbh increments, as potentially large errors can occur with infrequent remeasurement of trees using cloth tapes. This is particularly true in more mature stands with relatively small annual radial increments. ANPP from 1986 through 1989 was then calculated by adding the annual biomass changes to litterfall (see *Litterfall. . .*, below).

Needle elongation and new foliage accumulation rates.—To establish the rate of accumulation of new foliar biomass after bud-burst in the spring, we mea-

sured needle lengths on 15 branches from five trees in each of the central four plots (1–4: two control and two fertilized) using three metal towers in each. Trends observed on these plots were used to characterize elongation rates on all other control and fertilized plots. Measurements were made every 2 wk from March through June, and monthly thereafter. Relative elongation rates averaged over all canopy positions and trees were calculated as the fraction of the maximum for that year on a monthly basis. These fractions were used to adjust the new-foliage biomass from zero at bud-burst through the August sampling time, until the maximum was reached in the fall. Measurement of 1072 fascicles from the August 1986 destructive sampling showed strong linear correlations between needle length and needle area per fascicle for both two- and three-needle fascicles (e.g., $R^2 = 0.89$ for two-needle fascicles), supporting the use of relative needle length as a surrogate for relative canopy area or biomass of new foliage.

Litterfall and old foliage biomass decreases.—Litterfall was collected monthly from five 1 × 1 m traps in each of the 16 plots. Samples were separated into needles and other material, dried at 70°, and weighed to an accuracy of ±0.1 g. To calculate seasonal changes in old-foliage biomass, we added monthly needlefall from bud-burst until August to the August biomass values and then subtracted needlefall after August. We determined whether the litterfall values required correction for loss of mass prior to abscission by comparing measured, specific needle areas of freshly collected litter with old foliage still on the trees (see *Specific leaf areas . . .*, below).

Specific leaf areas: converting mass to area.—To convert from foliar biomass to area, we applied specific leaf areas (fresh leaf area per unit leaf dry mass, all-sided basis) measured on samples of new and old needles from plots 1–4 collected in the needle-elongation surveys and of dead needles from the litter traps. In August 1986 we subsampled our destructive samples and measured specific needle areas on 1072 fascicles. In October 1986, five fascicles of each age class from each of three canopy positions (lower, middle, upper) per tree were measured. In 1988 and 1989, 10 fascicles from the upper and lower crown were collected monthly from three replicates per plot. Similar sampling was carried out for fresh litterfall samples collected at the same time. All-sided leaf areas were calculated from needle volumes and lengths using the water immersion method (Johnson 1984). Conversions from an all-sided to a projected basis were made where necessary by dividing by 3.14 (Grace 1987).

Measurement of PAR penetration

We measured incident PAR (380–710 nm) on flat, horizontal surfaces above the canopy, directly beneath the live canopy, and at the shrub layer of our central four stands (plots 1–4, 2 control and 2 fertilized) using arrays of light-sensing diodes (GaAsP, Type #G1118 Photodiodes, Hamamatsu Corporation, Bridgewater, New Jersey) attached to tubular, triangular antenna towers. Each array consisted of 12 diodes on two perpendicular, horizontal booms 6.1 m long. Three diodes were spaced 0.5 m apart starting at the outside of each of the four boom arms, leaving a distance of 2 m between the innermost diode of each boom and the tower, to minimize artificial shading by the tower. Booms in all four plots were placed at the same azimuths so that any tower effect that did occur would be identical in all cases. The 12 diodes of each array were connected in parallel to an amplifier so that their averaged output signal could be recorded hourly using a standard data logger. Because the towers were also used to gain access to the canopy, and because of limited numbers of channels in the data loggers, the number of arrays was limited. In addition to an above-canopy array, plot 3 had two below-canopy arrays and three arrays at the shrub surface (one each on two towers and one located separate from a tower, all 2 m above ground). Plot 4 had one above-canopy array, and plots 1, 2, and 4 were equipped with one array each at the bottom of the canopy and one each at the shrub surface. The average of the two above-canopy arrays was used to characterize incoming PAR.

Diode arrays were initially calibrated against a LI-COR PAR line sensor under clear skies. The diode manufacturer's specifications indicated a highly linear response in the PAR range, which we verified through cross checks against LI-COR sensors under a range of conditions. Factory-calibrated LI-COR spot PAR sensors were also maintained at the top of the canopy to detect drift or degradation of the diode arrays.

The hourly, above-canopy, diode PAR data were closely related to the LI-COR spot sensor values (e.g., $R^2 = 0.99$, $n = 5034$ h from 21 December 1987 through 20 December 1988) and indicated no major shifts in calibration over the measurement period. However, the diode data were always lower than the LI-COR data, indicating that the initial calibration was precise but slightly biased. (The slope of the line relating diode to LI-COR data for the period above was 0.9286, and the intercept was −5.5.) Nevertheless, because all diode arrays were calibrated in the same way and at the same time, we feel that their values are directly comparable. With the above relationship we filled in any missing diode data to produce a continuous above-canopy hourly record from 7 November 1987 to 6 October 1989.

We preferred to compare above-canopy PAR to PAR directly below the canopy to minimize the additional effects of light interception by stems. However, we were restricted by the number of towers available for sensor support. Shrub-level and below-canopy-level data were highly correlated for arrays attached to the same tower, but they became more variable when a shrub array on one tower was contrasted with a below-canopy array

on another tower. In fact, we could not demonstrate any greater absorption of PAR at the shrub level than at the below-canopy level, and sensors at this level occasionally registered higher hourly values than sensors directly below the canopy. Unfortunately, all the arrays on a plot were connected to the same data logger so that, if below-canopy data were missing, shrub-level data were not recorded as well, and so no missing data could be approximated.

The following analyses are based on mean above-canopy data and mean below-canopy plus shrub-level data from plots 1–4, with all fertilized vs. control below-canopy comparisons made using means of data from plots 2 and 3 vs. plots 1 and 4. Our sample size was 672 daily values from 7 November 1987 through 6 October 1989 out of a total of 701 d. (Lightning damage prevented all below-canopy data logging from mid-July through mid-August 1988.)

Coefficients of light extinction (k) were then calculated for plots 1–4 assuming a Beer-Lambert law negative exponential relationship between LAI and light penetration:

$$I = I_0^{-k \cdot \mathrm{LAI}}, \tag{4}$$

where I_0 is incident PAR and I is the amount of incident PAR penetrating the canopy (Monsi and Saeki 1953, Kira et al. 1969). We summed daily above- and below-canopy PAR, applying the restriction that each day had to be represented by at least 4 h of continuous data, with at least one of those hours occurring between 1000 and 1400. Monthly LAI values were interpolated to daily values using a fourth-order polynomial with day of year as the independent variable.

Using direct-beam light penetration to estimate LAI

We also used the DEMON leaf-area measurement system (Assembled Electronics, Sydney, Australia; based on Lang and Yueqin 1986) to estimate projected LAI in early May and late July 1989 (the latter date corresponding to the time of the destructive biomass sampling in the previous 3 yr). On each plot, 20 random, 34-s transects were measured between solar-zenith angles of 20° and 80° under clear sky conditions. LAIs were calculated from the logarithm of average light penetration (relative to light in the open) with computer software (DEMSOFT) purchased with the DEMON. For comparison with our destructively obtained, all-sided LAI data, we multiplied the DEMON values by 2.0 (according to A. R. G. Lang, *personal communication*).

Remote sensing and LAI

The remotely sensed data we used were recorded by the Landsat Thematic Mapper (TM) (Curran 1985). The images were in digital form with each radiation value representing an area of $\approx 30 \times 30$ m on the ground. Three cloud-free images were selected from 26 February 1988, 21 September 1988, and 16 March 1989. Scenes were purchased with nearest-neighbor geometric correction. Image processing involved two stages: general radiometric and atmospheric correction, and specific processing comprising plot location, irradiance normalization, calculation of waveband ratios, and correction for the effect of solar-zenith angle.

Radiometric correlation involved the conversion of relative digital numbers (DN) in each wavelength to absolute radiance (L) in megawatts per square centimetre per steradian per micrometre:

$$L = \text{gain}\ (\mathrm{DN} - \text{offset}), \tag{5}$$

using the gain and offset data provided by the Earth Observation Satellite Company (Clark 1986). The atmospheric correction suppressed the effect of atmospheric scattering using the modified dark-object subtraction technique of Chavez (1988, 1989). First, the minimum radiance of deep lakes in the image was extracted, assuming that without atmospheric scattering the minimum radiance of these features would be zero. Second, a relative power-law scattering model was selected to represent the atmospheric conditions at the time that the images were collected, using the guidelines of Chavez (1988). This varies from the -1.0 power of the wavelength on moderately clear days to the -0.7 power on hazy days. Using the minimum radiance in green wavelengths as an arbitrary starting point, the model was applied relative to radiance in all wavelengths.

To establish plot location on the images, between 16 and 20 ground control points (e.g., road junctions, bridges, stand boundaries) were located on a topographic map and on each digital image of the study area. The pixel that was closest to the center of each plot was identified by triple triangulation from the relevant ground-control points, and the radiance was extracted. If repeated triangulation located two adjacent pixels for one plot, the mean radiance for the two pixels was used.

To suppress irradiance differences between images, the radiance can be normalized. This is typically achieved by calculating reflectance (Curran 1985), but in this case we wished to retain the original physical units of radiance. Therefore, the mean radiance of three road intersections in each image was used as a measure of relative irradiance with which to normalize all of the images to that recorded in February 1988.

Using the radiance (L) in the NIR and R wavebands, the normalized difference vegetation index (NDVI) was calculated as:

$$\mathrm{NDVI} = (L_{\mathrm{NIR}} - L_{\mathrm{R}})/(L_{\mathrm{NIR}} + L_{\mathrm{R}}). \tag{6}$$

Finally, NDVI was corrected for the effect of variation in solar-zenith angle (which is negatively related to NDVI) using a look-up procedure on the modeled data of Singh (1988). The results of the processing were one NDVI value per plot, per date.

TABLE 1. Regression coefficients for canopy components for each year. Equations are of the form: ln(biomass) = $a + b$ ln(dbh), where biomass is in grams per tree and dbh (diameter at 1.3 m height) is in centimetres.

Component	Year	a	b
A) Control trees			
New foliage	1986	0.0784	2.6784
	1987	−2.3607	3.4816
	1988	−0.7589	2.8780
Old foliage	1986	−0.2434	2.9451
	1987	−2.4845	3.5995
	1988	−1.9727	3.3916
New twigs	1986	−3.0211	3.2225
	1987	−6.7508	4.4883
	1988	−3.5803	3.3151
Old twigs	1986	−1.1417	2.7724
	1987	−5.2729	4.0574
	1988	−3.1225	3.3945
Unfoliated branches	1986	−1.8193	3.7325
	1987	−3.6388	4.3057
	1988	−0.8522	3.3005
B) Fertilized trees			
New foliage	1986	0.5677	2.4835
	1987	−1.4007	3.1693
	1988	−3.4643	4.0157
Old foliage	1986	0.3155	2.7460
	1987	−1.3488	3.2235
	1988	−1.8585	3.4732
New twigs	1986	−0.8077	2.4063
	1987	−3.1056	3.2117
	1988	−4.7751	3.8807
Old twigs	1986	−0.0188	2.3594
	1987	−3.3773	3.4506
	1988	−4.1678	3.8671
Unfoliated branches	1986	−2.5294	4.0119
	1987	−2.1295	3.7637
	1988	−1.4016	3.5420

TABLE 2. Canopy regression parameters pooled over treatment for 1986 through 1988, as used for final biomass calculations (non-pooled equations are in Table 1). Equations are of the form: ln(biomass) = $a + b$ ln(dbh), where biomass is in grams per tree and dbh (diameter at 1.3 m height) is in centimetres.

Component	Year	a	b
New foliage	1986	0.4731	2.5253
	1987	−1.6617	3.2491
Old foliage	1986	−0.0220	2.8639
	1987	−2.1051	3.4608
	1988	−1.8616	3.4131
New twigs	1986	−1.8752	2.7911
	1987	−4.3575	3.6502
Old twigs	1986	0.9285	1.9894
	1987	−4.1893	3.6943
	1988	−3.7105	3.6534
Unfoliated branches	1986	−2.3577	3.9406
	1987	−2.6326	3.9486

RESULTS

Annual canopy biomass estimation from destructive sampling

Parameters of the August canopy-biomass regression equations exhibited several distinct patterns (Table 1). In all cases changes in the slopes and intercepts were inversely related. For control trees, the 1987 slope of each line increased relative to the 1986 slope, and the 1988 slope decreased, less dramatically, relative to 1987. Y intercepts decreased in 1987 and increased again in 1988. However, statistical analyses showed no significant differences among the parameters (at $P = .05$), within either treatment, from year to year, although several were significant at the $P = .10$ level. For the purpose of computing August biomass for 1986, 1987, and 1988, we kept each year's data separate in spite of the lack of significant statistical effects of year.

Both increases in dbh and changes in the slope or intercept of the regression could lead to changes in estimated biomass. For example, application of a single equation for new foliage, based on pooled tree data for control plots from all 3 yr, produced average increases of 65 kg/ha from 1986–1987 and 128 kg/ha from 1987–1988 due to dbh changes alone, rather than decreases of 48 and 269 kg/ha as we would have estimated using the separate equations for each year.

There were no significant effects of the fertilization on tree biomass relative to control plots except for new foliage in 1988. Therefore, except for the new foliage in 1988, data for the same tissue within a year were pooled over treatment and new regressions were run for the pooled data (Table 2). However, because the amounts of foliage and twigs were highly correlated, we also kept the new twig and branch equations separate for 1988 even though relatively large variances led to no statistically significant effects of the fertilization on these tissues.

Application of the regression equations to the plot diameter data indicated that estimated biomass of new foliage decreased by 317 kg/ha from 1986 through 1988 on the control plots (Table 3A). Foliage biomass on fertilized plots in 1988 was about twice that of the control plots. Old foliage decreased >1100 kg/ha from 1986–1987, but recovered about half this amount in 1988. The net effect was less total foliar biomass in 1987 and 1988 on control plots than in 1986, and a large increase in 1988 in fertilized plots to levels ≈1100 kg/ha greater than the control plot values of any year.

LAIs decreased 13% from August 1986 to 1987 across all plots. From 1987 to 1988, LAI slightly increased on control plots and increased an additional 40% on fertilized plots (Table 3A). The drop from 1986 to 1987 was due to decreased old foliage, whereas changes in old and new foliage largely offset each other from 1987 to 1988. As already discussed, the increase on the fertilized plots in 1988 was due to greater new-foliage production rather than to increased retention of old foliage.

TABLE 3. Biomass and production of fertilized (F) and control (C) slash pine stands. Data are means, with 1 SD in parentheses.

A) Canopy biomass (kg/ha) and leaf area index (LAI) in August for each year and treatment.

Component	Year*			
	1986 (C & F)	1987 (C & F)	1988 (C)	1988 (F)
New foliage	2505 (297)	2457 (295)	2188 (356)	4141 (381)
Old foliage	4054 (499)	2919 (359)	3486 (454)	3486 (454)
Total foliage	6559	5376	5674	7627
LAI—new	2.60 (0.31)	2.72 (0.34)	2.34 (0.38)	4.49 (0.41)
LAI—old	3.39 (0.43)	2.53 (0.31)	2.96 (0.38)	2.96 (0.38)
LAI—total	5.99	5.25	5.30	7.45
New twig	515 (63)	533 (67)	468 (80)	750 (67)
Old twig	847 (95)	717 (91)	1112 (149)	1112 (149)
Unfoliated branch	8912 (1247)	7146 (931)	6863 (1174)	8077 (663)
Twig & branch—total	10 274	8396	8443	9939

B) Stem biomass (kg/ha) in August for each year and treatment.

Component	Year							
	1986 (C)	1986 (F)	1987 (C)	1987 (F)	1988 (C)	1988 (F)	1989 (C)	1989 (F)
Wood	83 900 (13 400)	82 900 (6000)	88 000 (14 200)	86 600 (6100)	91 000 (14 000)	92 200 (6300)	95 900 (16 300)	97 500 (6600)
Bark	15 500 (2300)	15 300 (1000)	16 000 (2400)	15 800 (1100)	16 400 (2300)	16 600 (1100)	17 100 (2600)	17 300 (1100)
Total	99 400	98 200	104 000	102 400	108 500	109 000	113 000	114 800

C) Mean litterfall, total biomass increments, and aboveground net primary production (ANPP) (all in $kg \cdot ha^{-1} \cdot yr^{-1}$) for August–July intervals by treatment (ANPP = litterfall plus biomass increment).

Variable	Year*					
	1986–1987 (C)	1986–1987 (F)	1987–1988 (C)	1987–1988 (F)	1988–1989 (C)	1988–1989 (F)
Litterfall						
Needles	3642		4043		3247	4512
Total	4362		4870		4216	5888
Biomass increment						
Foliage	−1183	−1183	+298	+2251	0†	0†
Twig & stem	+2722	+2322	+4547	+8143	+4500†	+5800†
ANPP	5901	5501	9715	15 264	8716	11 680

* n = 7 control and 8 fertilized plots in 1986, and 8 control and 8 fertilized plots in 1987–1989.
† Biomass increment of twigs and foliage assumed = 0.

Seasonal canopy dynamics

Needle-elongation rates were similar for the control and fertilized plots monitored in 1987–1988 (Fig. 1), and data were pooled to obtain averages for that year. Differences between elongation rates were observed in 1988–1989 and 1989–1990, with fertilized trees breaking bud ≈2 wk earlier and elongating much faster. In all cases, bud-burst occurred in early to mid-March and needle growth continued until mid- to late October. No significant elongation took place under any conditions after October. These patterns demonstrate that the August destructive samplings occurred when the new foliage was 75–80% elongated.

Litterfall peaked between late October and early December, when over half the annual amounts fell. Patterns of cumulative needle litterfall were very similar over the 3 yr and for both treatments (Fig. 2). For the measurements in 1986–1987 (not shown) and throughout 1987–1988, cumulative litterfall on the control plots was higher than on the fertilized plots. (The difference was not significant at $P = .05$.) However, needlefall for the fertilized plots exceeded that for the control plots beginning in June 1988 and stayed higher throughout that year and 1989–1990 (Fig. 2). Needles comprised 83% of the annual total litterfall in 1986–1987 and 1987–1988, and 77% of the total in 1988–1989 in both control and fertilized plots.

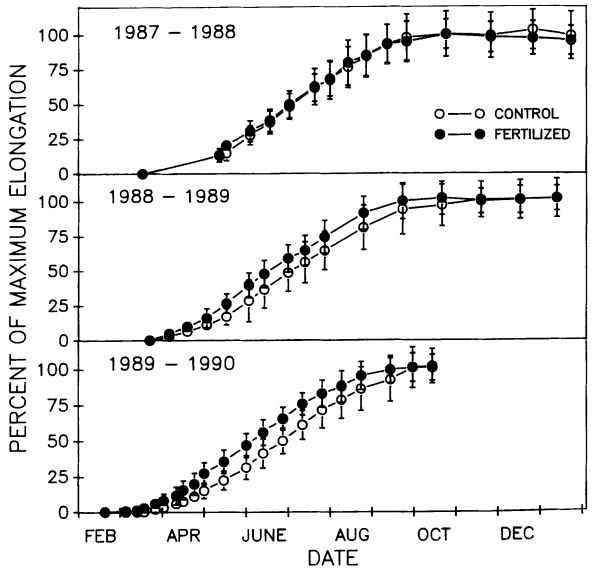

FIG. 1. Relative needle-elongation rates (means ± SD) for control (plots 1 and 3) and fertilized (plots 2 and 4) treatments.

Specific leaf areas of the litter and old foliage from samples collected at the same time from each plot (Fig. 3) were not significantly different (old foliage, 89 ± 5 cm^2/g [$\bar{X}$ ± SD], $n = 228$; litter 84 ± 4 cm^2/g, $n = 68$). Therefore, an average specific leaf area of 86 cm^2/g was applied to old foliage and to litter to compute the decline in LAI for old foliage from litterfall-mass measurements. Initially high specific leaf areas of new foliage decreased over the season (Fig. 3). There was some effect of treatment and canopy position, but because the differences were not consistent we used average values for each date to characterize the seasonal changes for new foliage.

Seasonal patterns of LAI for the individual foliage cohorts (Fig. 4 top) supported our use of separate August regression equations for the 3 yr. For example, estimates based either on the August 1986 or 1987 destructive samplings produced identical cohort-2 leaf areas for March 1987; March 1988 cohort-3 values differed more, depending upon whether they were calculated using August 1988 or 1987 data, but were still within 10% of each other. The maximum fertilization effect on cohort 4 over 1988–1989 was a 69% increase.

The August destructive data indicated a decreasing LAI of control plots over the 3 yr, from 6.5 to 5.5 to 4.8 (Fig. 4 bottom). The composite August data, needle-elongation data, and litterfall data produced a seasonal pattern of an early fall maximum LAI, decreasing about 40% to a late winter minimum. Average seasonal minima and maxima for control plots were 4.3 and 6.5 in 1986–1987 (using March 1987 as the minimum), 3.5 and 5.6 in 1987–1988, and 3.0 and 5.3 for control plots in 1988–1989. Fertilization apparently led to a maximum LAI in August 1989 and that was 41% greater than the control plot average at the same time.

Annual stem growth and ANPP

Because dbh either stays the same or increases year to year relative to initial diameter, stem biomass accumulation patterns are highly sensitive to stem biomass at the beginning of the study. Therefore, because the plots varied widely in initial stem dimensions, we maintained control and fertilized plots separate for all 3 yr in computing stem biomass. Initial averages over all plots were similar, although the control plots were much more variable than the fertilized plots (Table 3B). From 1980–1981 through 1986–1987, average, annual, stem-wood biomass increments were greater for control plots than fertilized plots (Fig. 5). However, increments for 1987–1988 and 1988–1989 were much higher for fertilized plots. Increments of bark biomass were much lower and showed little difference between treatments over time.

Annual ANPP was calculated by adding biomass increment and litterfall (Table 3C), ignoring the minor components of herbivory and leaching of organic compounds (Cole and Rapp 1981). The assumption of a steady-state canopy leads to the simplification of having to account only for stems in terms of increments, but is clearly inappropriate in our case.

Total litterfall and stem-biomass increments covered similar ranges during the study. Large increases in both canopy and stem biomass were largely responsible for ANPP values for fertilized plots that were >4200 $kg \cdot ha^{-1} \cdot yr^{-1}$ greater than for control plots in 1987–1988 and 1988–1989. The control plot values

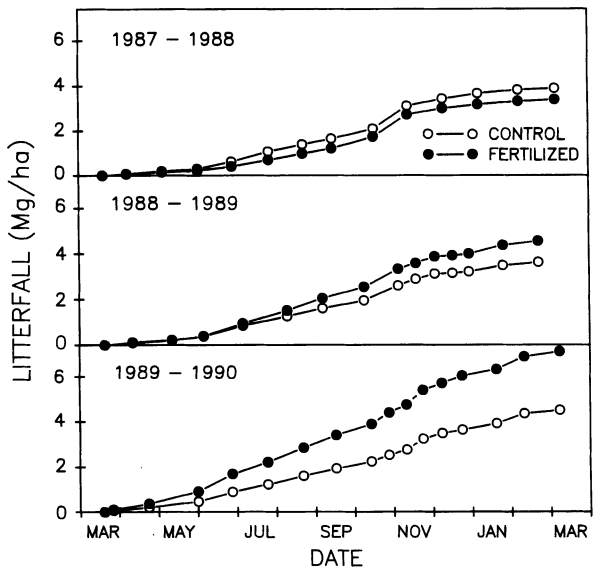

FIG. 2. Cumulative needle litterfall for control and fertilized plots (treatment means; $n = 8$ plots each).

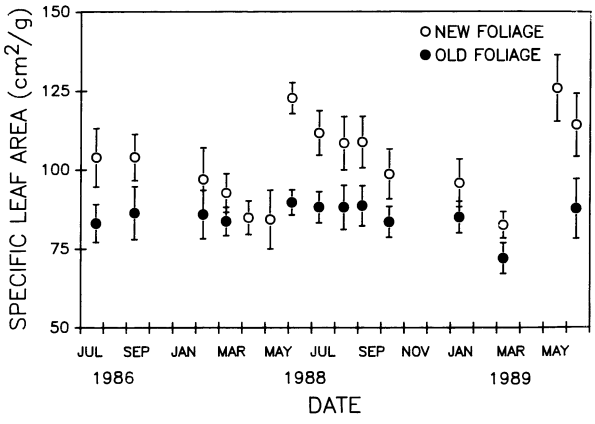

FIG. 3. Seasonal specific needle (leaf) areas for new and old foliage.

are similar to those previously reported for other unfertilized stands of similar age (Gholz and Fisher 1982). Due to offsetting changes in the components, the ANPP even of the control plots steadily increased from 1986–1987 through 1988–1989, even though the general trend of stem-biomass increments with age was a steady decline (Fig. 5). ANPP varied by a factor of three across the two treatments and 3 yr.

Light attenuation through slash pine canopies

The maximum values of daily integrated PAR at the top of the canopy showed a strong seasonal pattern with substantial daily variation (Fig. 6 top). Light penetration through the canopies also varied seasonally, with 31% (ranging from 18 to 42% at the various plots) of incident PAR reaching the below-canopy arrays, although daily variation was much less than for incident PAR (Fig. 6 bottom). For the year 21 December 1987 through 20 December 1988, canopy absorption of the incident photon flux averaged over the four plots was 8086 mol/m^2. Minimum penetration occurred in early winter and the maximum in early summer, out of phase with seasonal LAI but corresponding directly to incident PAR. Variation was greatest during winter. We could detect no effect of the fertilization on the relative light penetration. For example, from 11 July 1989 through 6 October 1989, when a fertilizer effect should have been at its maximum, with both age classes of foliage affected and needles fully expanded, the mean differences in hourly incident PAR between the two below-canopy sensors on plot 3 (control) and the one on the neighboring plot 4 (fertilized) were only 10.5 and 38.7 μmol·m^{-2}·s^{-1}, with neither significantly different from zero (t test, $P = .05$, $n = 736$ and 795 h, respectively).

To generalize the pattern of light penetration, we fitted a sine function to the data averaged over all four plots (Fig. 6 bottom):

$$\text{FBC} = \sin[(\text{day} + 275)\cdot(\pi/190)]\cdot 0.888 + (0.32 - \text{day}\cdot 0.0001), \quad (7)$$

where day = 1 corresponds to 7 November 1987 and FBC is the fraction of incident PAR received below canopy ($R^2 = 67$, $n = 672$ d). The 0.0001 value in the equation produces a decreasing mean over the 2 yr (Fig. 6).

Daily light-extinction coefficients (k) from the Beer-Lambert law (Eq. 4) were calculated from equation 7 and daily LAI values (all-sided) were obtained using linear interpolations between monthly estimates and averaging over all plots (since no fertilizer effect was detected). Resultant k values ranged from 0.17 in mid- to late summer, to 0.35 in fall and spring (Fig. 7).

Direct-beam radiation penetration and LAI

Our last destructively based data point for LAI was from 27 March 1989. Therefore, to obtain values to compare with the DEMON results we assumed that the amount of new foliage produced in 1989 was the same as in 1988, and used our relative elongation data and litterfall measurements to compute expected values of LAI for early May and late July. (The estimates for new-foliage production can eventually be verified through litterfall measurements.) Because new foliage was more developed in July, possible errors due to this approximation should be greater at that time.

In May the DEMON system apparently overestimated average LAIs on the control plots by 40% and fertilized plot averages by 15% (Table 4). In July, the DEMON system underestimated LAI by 6% for control plots and 15% for fertilized plots. Therefore, except

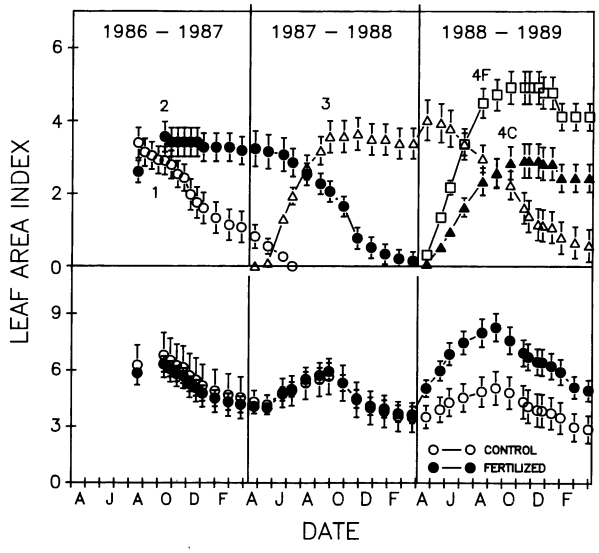

FIG. 4. Top panel: Leaf area index (LAI) for four foliage cohorts (1 ○; 2 ●; 3 ▲; 4 □, ▲). F = fertilized, C = control. Bottom panel: Total LAI for the slash pine stands over three years.

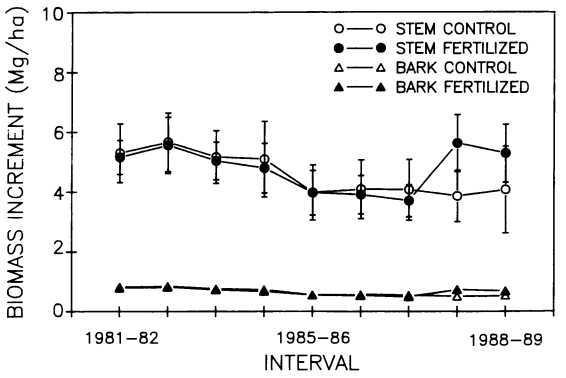

FIG. 5. Annual increments of both stem-wood and bark biomass (means ± SD) for control and fertilized plots, computed using increment core data and the 1987 diameter-at-breast-height inventory as the base line.

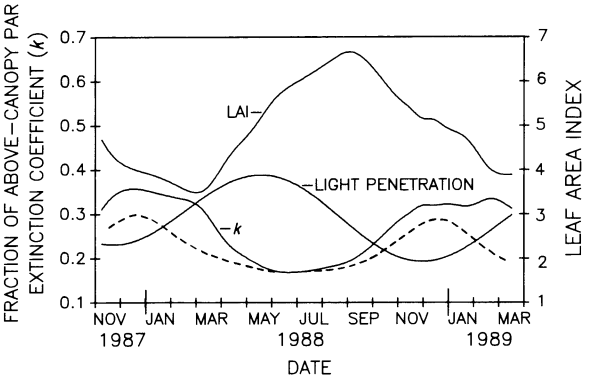

FIG. 7. Light-extinction coefficient (k) values, computed from the smoothed all-sided leaf area index (LAI) and light-penetration data. The dashed line represents $k = 0.17$ (June 1988) corrected by cosine of the noon solar-zenith angle.

for the May control plots, the comparison of mean values was reasonably good.

Remote sensing and LAI dynamics

There was a positive, linear relationship between LAI and NDVI of the 16 plots on the three dates (Fig. 8), with R^2 values of 0.35, 0.75, and 0.86 for February 1988, September 1988, and March 1989, respectively. Linearity was expected because the reflectance asymptote for conifer canopies is usually reached at LAI values far in excess of those recorded in this study (Peterson et al. 1987, Herwitz et al. 1990). The relationships between NDVI and LAI appear similar for the three dates, but both the constants and the NDVI coefficients differed from each other at the 0.95 level of significance (F test). These differences can be attributed to measurement error and probable differences in atmospheric conditions and understory ground cover at the time of image acquisition (Fraser and Kaufman 1985, Curran and Williamson 1987, Spanner et al. 1990).

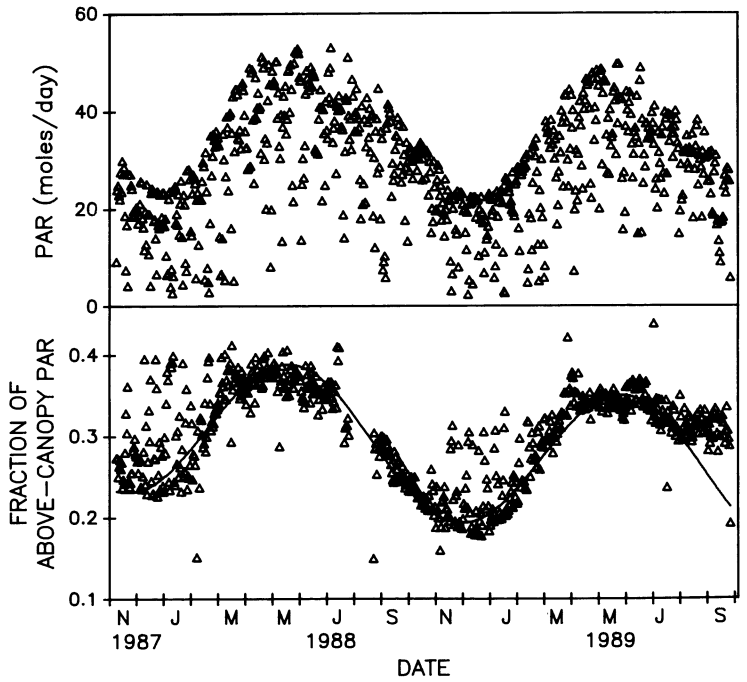

FIG. 6. Daily above-canopy incident photosynthetically active radiation (PAR; top panel) and relative light penetration (below-canopy PAR divided by above-canopy PAR) through the slash pine canopy (bottom panel).

TABLE 4. Leaf area index (LAI) (all-sided) estimated with the DEMON system on 3–5 May 1989 and 28–31 July 1989 vs. LAI ("mass balance"), estimated by subtracting litterfall and adding new-foliage production to late March 1989 measured LAI (assuming 1989 new-foliage production was the same as for 1988). F = fertilized; C = control. Data are means ± SD.

Plot	DEMON system LAI		Mass-balance LAI	
	May	July	May	July
1F	5.88 ± 0.22	5.52 ± 0.24	5.61	7.49
4F	6.06 ± 0.30	6.86 ± 0.34	4.57	5.81
6F	5.66 ± 0.18	6.32 ± 0.48	5.78	7.55
8F	6.16 ± 0.28	5.64 ± 0.16	6.48	8.52
10F	5.62 ± 0.38	6.08 ± 0.96	4.76	6.15
11F	6.62 ± 0.30	5.64 ± 0.16	4.76	6.05
14F	6.12 ± 0.26	4.76 ± 0.24	5.08	6.48
15F	6.52 ± 0.24	6.30 ± 0.18	5.05	6.41
2C	4.40 ± 0.28	4.40 ± 0.38	3.05	3.78
3C	5.20 ± 0.18	4.50 ± 0.24	2.06	2.54
5C	5.28 ± 0.16	4.56 ± 0.16	3.74	4.54
7C	5.38 ± 0.20	4.91 ± 0.14	4.44	5.61
9C	5.52 ± 0.30	4.70 ± 0.50	4.63	5.64
12C	5.04 ± 0.26	3.52 ± 0.12	4.04	5.06
13C	4.98 ± 0.24	3.46 ± 0.74	4.03	4.76
16C	5.78 ± 0.42	4.38 ± 0.18	3.75	4.58
C plots	5.20 ± 0.42	4.30 ± 0.54	3.72 ± 0.82	4.56 ± 1.02
F plots	6.08 ± 0.36	5.90 ± 0.64	5.26 ± 0.65	6.81 ± 0.94

Using data from half of the plots (1 to 8), three predictive relationships (Table 5) were derived to estimate the LAI of the other plots (9 to 16), and the results were compared over all three dates (Fig. 9). Root-mean-square error of the comparison (Fig. 9) was 0.74 LAI (16% of the mean LAI).

DISCUSSION

Estimating foliar biomass and LAI from destructive harvests

Our intensive sampling with destructive harvests demonstrated that subtle but potentially important differences in major components of canopy biomass can occur from one year to the next. One way of determining whether interannual differences in LAI are real or sampling artifacts is to compare the new foliar biomass in March at the end of one measurement year, based on the subsequent August destructive sampling and needle-elongation data, and cumulative needle litterfall over the next measurement year. For example, we estimated cohort-2 foliar biomass in March 1987 to be 3477 kg/ha averaged over all the plots, and the following year we collected an average of 3641 kg/ha needle litterfall from these plots. Likewise, we estimated cohort-3 foliar biomass in March 1988 to be 3930 kg/ha and collected 4085 kg/ha litterfall over the next year, and estimated cohort 4 as 3412 kg/ha and measured 4526 kg/ha litterfall. However, in March of all 3 yr we estimated some residual (>2-yr-old) foliage mass which should also have fallen off during the ensuing year. These residuals were 1300 kg/ha for cohort 1 in 1987, 389 kg/ha for cohort 2, and 1028 kg/ha for cohort 3. When the residuals are added to the old-foliage biomass and then compared to litterfall over

TABLE 5. Predictive regression equations for plots 1 to 8 on three dates: LAI = $a + b$·NDVI, where LAI = leaf area index and NDVI = normalized-difference vegetation index. These equations were used to estimate the LAI values in Fig. 9.

Date	n	a	b	SE of estimate	R^2
February 1988	8	−14.31	32.25	0.33	0.86
September 1988	8	−20.02	43.62	0.82	0.82
March 1989	8	−10.80	26.29	0.52	0.83

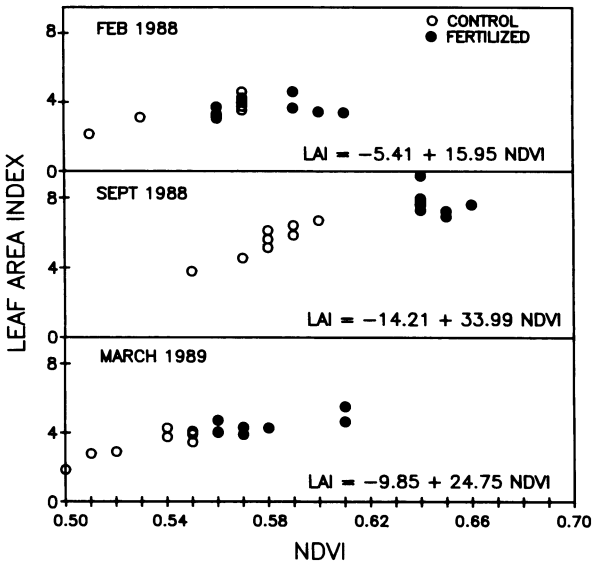

FIG. 8. The relationship between the normalized difference vegetation index (NDVI) recorded by the Landsat Thematic Mapper and the leaf area index (LAI) for sixteen plots on 26 February 1988, 21 September 1988, and 16 March 1989.

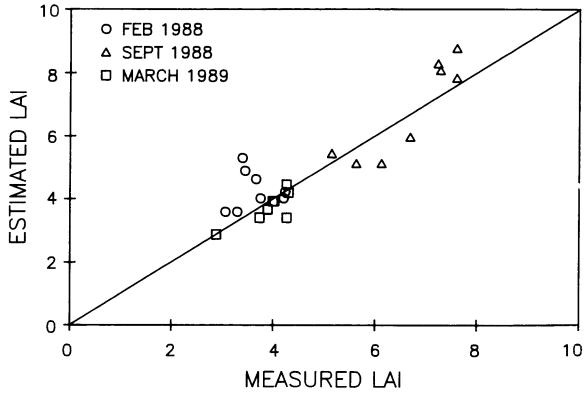

FIG. 9. The relationship between the measured and estimated leaf area index (LAI) for four control and four fertilized plots for three dates (see Fig. 8) for which remotely sensed data are available. The estimated LAI was derived from three predictive regression relationships, each based on four control and four fertilized plots (Table 5).

the next year, the differences were +1136, +234, and −86 kg/ha over the 3 yr. Because litterfall can be measured rather precisely, we feel that this comparison validates our foliar biomass estimates for the second and third years, but indicates that the first-year estimates of cohorts 1 and/or 2 were too high. This also indicates that a substantial amount of >2-yr-old foliage can remain on the trees after March, depending on the year.

To determine if stand density or relative elevation (i.e., distance above the water table) among the plots led to the apparent overestimate of the August 1986 cohort biomass by significantly biasing the biomass per tree, we used stepwise multiple regression to examine individual tree data for each year. There were no significant effects ($P < .05$) of either density or elevation for any of the years. We must therefore conclude that either the trees selected in 1986 were not representative for some other reason or that our sample size in 1986 was simply too small to characterize accurately the variation among foliage biomass on trees of the study plots in that year.

The consistently higher litterfall rates on fertilized plots during 1988 were not reflected in differences in the old-foliage biomass of the trees that were destructively sampled in August. However, the cumulative difference in litterfall between fertilized and control plots in March 1989 was 1265 kg/ha. This indicates our assessment that the old foliar biomass levels on control and fertilized plots were not significantly different, based on the August 1988 destructive sampling, was too conservative; had we sampled later in 1988 significant differences would have been more likely.

Validation of foliar dynamics using light penetration

Daily light-extinction coefficients (k values) range from a low of 0.54 in June 1987 to 1.16 in December 1987 (projected-LAI basis). The June value is similar to the value of 0.52 presented by Jarvis and Leverenz (1983) as a mean for forests at zero zenith angle. However, there are few k values that have been generated from long-term field observation for comparison.

Sinclair and Knoerr (1982) estimated a variable hourly k value of 0.46/cos zenith angle in degrees for a loblolly pine plantation in North Carolina. In this case, with zenith angles of 5°, 45°, and 80°, their k would equal 0.46, 0.65, and 2.65, respectively. Pierce and Running (1988) used measurements of the below-canopy to above-canopy PAR ratio and an assumed k value of 0.52 to predict LAIs for a variety of *Pinus cortorta* stands in Montana. From measurements made between 9–22 September 1987 at 1200 and 1400, they concluded that k and light penetration were independent of solar-zenith angle, and that accurate estimates of LAI could be obtained for their stands from the assumed k and PAR measurements.

Extensive field measurements cannot always be avoided, however. If we assume that the value of k for mid-June (0.17 on an all-sided area basis) for our stands is an annual minimum, we can calculate cosine-corrected values for the rest of the year to compare with our derived values from the field measurements. However, the selection of the appropriate solar-zenith angle for use with summed daily radiation data has a great effect on the results. For example, zenith angles at noon vary from 5° in June to 53° in December, whereas mean daily zenith angles range from 44° to 72°. The use of noon zenith angles produces a range in k from 0.17 to 0.29 in June and December (Fig. 7). The use of mean daily zenith angles leads to a range in k from 0.24 in June to 0.56 in December. In neither case do the results match the field data over the year, even for the primarily clear sky conditions used to derive the curves in Fig. 7. This indicates that a cosine-corrected k based on limited field sampling does not adequately describe seasonality of canopy dynamics for this ecosystem. However, this does not preclude the derivation of a statistical best fit to the k data in Fig. 7, which may provide a useful index of a seasonally varying k for these stands.

In any case, the application of Beer-Lambert's law to a heterogeneous medium such as a forest canopy is tempting but questionable. Several alternative, though usually very complex, models have been proposed (e.g., Norman and Jarvis 1975, Kellomäki and Oker-Blom 1983, McKelvey 1990). Oker-Blom (1985) argued that it is necessary to account for branch position and penumbral effects around branches in order to model radiation interactions in a Scots pine canopy accurately.

Light penetration through slash pine canopies follows a highly predictable pattern that may have more to do with the fixed spatial distribution of trees and their foliage than with seasonal changes in LAI or biomass (Fig. 7). This, in addition to our inability to detect proportional differences in PAR absorbed between

control and fertilized plots regardless of a clear difference in LAI, means that the assumptions of the Beer-Lambert law may not be satisfied by slash pine canopies, and that the development of alternate approaches to modeling canopy structure and light penetration is justified. However, we should note that the apparent decline of ≈5% in penetration over the 2 yr (Fig. 6) is likely due to a fertilizer effect on LAI that we could not measure accurately enough to identify statistically.

There is a high degree of aggregation in slash pine canopies, with foliage concentrated into highly conical crowns, and within crowns into dense clusters of needles at the ends of branches. Because of this highly clustered nature a great deal of horizontal heterogeneity is observed, especially at low solar-zenith angles. The Beer-Lambert "law" must be restated to reflect this heterogeneity in light-penetration patterns. If we assume that where foliage exists attenuation is constant and follows the Beer-Lambert law, then light penetration for the canopy can be stated:

$$I_i = I_0 (F_o + F_f e^{-k \cdot \mathrm{LAI}}) \quad (8)$$

where I_i is below-canopy PAR, I_0 is incident PAR, F_o is the fraction of open sky, F_f is the fraction of foliated sky, and LAI is the generalized leaf area index for the canopy. (A form of this equation was first presented by Jackson and Palmer 1979.) If horizontal heterogeneity is ignored, the equation reverts to Eq. 4. We can then state that horizontal heterogeneity has two effects on light penetration. The first is that I_i computed using Eq. 8 is greater than that computed by Eq. 4 for all LAIs. The second is that shifts in LAI will have less impact on I_i in Eq. 8 than in Eq. 4. If we observe the behavior of Eqs. 8 and 4 at the limit LAI $\rightarrow \infty$, Eq. 8 approaches $I_0 \cdot f_o$, whereas Eq. 4 approaches zero.

Using this analysis, we can explain conceptually the behavior of seasonal light penetration through slash pine canopies. About 40% of the light emanating from low solar-zenith angles penetrates the canopy due to the large gaps between foliage clusters. At higher zenith angles the number of tree crowns—and therefore the number of clusters that a beam must pass through to reach the forest floor—increases. This increase in the effective number of clusters decreases the area of open sky, and therefore decreases light penetration. Thus, the system is very sensitive to the position in the sky from which light is emanating. Because the daily integral of direct-beam radiation is dominated by the period around solar noon, direct-beam radiation through slash pine canopies is largely coupled to the zenith angle near solar noon (hence the better correlation of cosine-corrected k values to measured k values in the summer and using noon zenith angles; Fig. 7).

Seasonal shifts in leaf area due to the growth and abscission of needle cohorts do not change the basic geometry of the stand. These processes change LAI in the foliated region of the sky rather than the occupancy of sky area. As was demonstrated (Eq. 8), the system is relatively insensitive to these changes. Effects of fertilization on light penetration would also be minimal as long as the population of needle clusters is not greatly changed by fertilization. Our data indicate that the greatest response to fertilization has been an increase in needle length rather than in number of clusters, although this may change over time as branch bifurcation increases. The lack of observed increase in light attenuation on fertilized plots supports this interpretation.

Our evaluation of the DEMON system for estimating LAI is equivocal. The method provided mean treatment LAIs for both May and July within 1 SD of our estimated values. However, it indicated a much narrower range in LAI, and, within this range, did not always provide values for specific plots that were close to the estimated values. The apparently low sensitivity of the DEMON system may be due, as explained above in this section, to foliar clumpiness. This should also lead to a general underestimation of LAI by the DEMON system because fewer than the actual number of needles in the canopy are sensed. The lack of consistency with estimated values may reflect measurement errors associated either with our use of the DEMON system or with our estimation of LAI.

The DEMON measurements also include some absorption by nonfoliar surfaces, though, which should compensate somewhat for clumpiness. Assuming that slash pine branches are long cones normal to incoming light, we calculated (using unpublished data) a maximum branch area index of 0.12 for these stands. Adding to that an estimation for light interception by stems equivalent to 0.19 LAI (McKelvey 1990), woody tissues should have an equivalent LAI of ≈0.30, which would not normally change much seasonally or over a few years. An effect of this magnitude appears to be within the bounds of measurement error for these stands and does not seem to have provided any consistent bias to the DEMON data; subtraction of this amount from the May estimates would create values closer to our estimates, but would make the July differences larger.

Remote sensing of LAI

The application of remote sensing to the estimation of forest LAI has been hampered by the need to measure LAI (or similar measures of foliar mass) accurately (Curran and Williamson 1985). Despite the logistical problems involved, several groups have managed to produce predictive relationships (e.g., Jensen and Hodgson 1985, Badhwar et al. 1986*a*, 1986*b*, Running et al. 1986, Danson 1987, Running et al. 1989, Herwitz et al. 1990, Spanner et al. 1990). For example, Peterson et al. (1987) reported a correlation coefficient between LAI and NIR/R of 0.95 for forests in the Pacific Northwest.

However, in all cases the power of these relationships

is made possible by including a very wide range of vegetation types or LAIs. More important, the ground data upon which these reported relationships are based used LAI measurements that were inherently unresponsive to seasonal changes. For example, most were derived using regression relationships between leaf area (or mass) per tree and a relatively stable tree dimension (e.g., dbh), with both variables collected at various times throughout the growing season and often in different years (e.g., the compendium in Gholz et al. 1979). Therefore, such relationships, although potentially useful for the estimation of LAI over large areas, cannot be used to evaluate the seasonal dynamics of any single forest stand.

The relationships illustrated in Fig. 8, in which remotely sensed data are related directly to a measured LAI during the month of satellite overpass, are the first published of their kind. Through their tracking of the LAI increase from February to September and decrease from September to March (Fig. 9), they demonstrate the potential value of Landsat TM data for the estimation of seasonal changes in a single forest type.

Four further observations can be made about the nature of the relationships between LAI and NDVI and potential further research. First, once the fertilized plots had a higher LAI than the control plots, they could be discriminated on the basis of NDVI. Some of the fertilized plots were clearly visible on false-color Landsat TM imagery for February 1988 and March 1989, and all of the fertilized plots were clearly visible in September 1988. Second, as a result of the fertilization, the LAI of the understory increased with the LAI of the canopy (D. Guerin and H. Gholz, *personal observation*). Therefore, some of the NDVI values may have been inflated relative to the canopy LAI when the canopy LAI was low. Future work using spectral-mixture models will enable us to evaluate the magnitude of this influence (e.g., Curran et al. 1990). Third, it should be possible to estimate retrospectively the seasonal patterns of LAI in these stands over many previous years using the relationships demonstrated here and readily available TM imagery. Fourth, once the relationships between LAI and NDVI have been obtained, they could be used along with readily available Landsat TM imagery as drivers for seasonally sensitive ecosystem models over a number of years and, potentially, over many different stands.

Controls over slash pine LAI

Can our empirical view of slash pine canopy dynamics be used to derive more flexible and accurate predictive models of LAI dynamics? Models of "maximum LAI" from the Pacific Northwest (e.g., Gholz 1982, Grier and Running 1982) have been effective because they incorporate a very broad range of vegetation types and LAIs that are related to correspondingly broad patterns in water availability. Slash pine grows naturally on sites characterized by sandy soils, but with a permanent water table within reach of the roots of mature trees. Even though relatively high atmospheric vapor deficits can develop, stands have low LAIs and low transpiration rates (H. L. Gholz et al., *unpublished data*), and there seems to be little interaction between water availability and LAI. Obviously, nutrition maintains a strong control over LAI, but we cannot yet develop a predictive relationship with only one nutritional treatment.

However, we have enough data from >5 yr of litterfall collections from this study (3 yr) and a previous study (2 yr) on similar sites (Gholz et al. 1985*b*) to characterize seasonal patterns and to explore the relationship of needle litterfall for unfertilized stands to climatic conditions. Because slash pine foliage has two principal age classes, litterfall collections should reflect foliage production from the previous year.

Cumulative litterfall data can be fit to a logistic regression equation:

$$Y_t = K/[1 + \exp(c - rt)], \quad (9)$$

where Y_t is the cumulative litterfall at time t; K, c, and r are parameters fit from nonlinear regression; and t is time. (This approach has also been successfully applied to *Pinus taeda* by Dougherty et al. 1990.) This model provided an excellent fit to the data in Fig. 2, where t was defined as the number of days elapsed from March 1, with correlations between predicted and observed values consistently >0.99. The variation among the parameters of the logistic model (K ranged from 327 to 571, c from 3.07 to 4.26, and r from 0.014 to 0.019) also provided the opportunity to develop predictive models for these parameters.

We first needed to account for differences in initial foliar biomass among the stands for which we had litterfall data. Since foliar biomass per tree is relatively insensitive to variation in stand density under a normal range in stocking (this study, and Gholz and Fisher 1982), we accomplished this by including stand basal area as a variable in the model. We then included various climate variables from the spring and summer of the year before the litterfall was collected. We chose these intervals as most likely to be associated with rates of needle growth and development for this same cohort. Finally, we used a stepwise multiple linear regression analysis to select the best model for each parameter based on an F test for each variable.

In addition to basal area, selected each time, the analysis identified April–June growing degree days (base: 10°) and total incoming solar radiation as the most significant independent variables (all with significance levels ≤.06). Precipitation, pan evaporation (ET), and ET-precipitation did not meet the significance criterion ($P = .05$) for inclusion in the models. The resultant predictive equations for the logistic parameters were:

$$K = -960.36 + 9.65 \cdot BA + 0.51 \cdot GDD; \quad R^2 = 0.69, F = 15.6 \quad (10)$$

$$c = 3.2085 - 0.0503 \cdot BA + 0.0026 \cdot SR; \quad R^2 = 0.70, F = 13.0, \quad (11)$$

and

$$r = 0.0360 - 0.0002 \cdot BA - 0.0000104 \cdot GDD + 0.0000137 \cdot SR; \quad R^2 = 0.77, F = 14.3, \quad (12)$$

where: BA is the stand basal area per unit ground area (m^2/m^2), GDD is the growing-degree-day sum for April through June, and SR is the average monthly total incoming solar radiation (in megajoules per square metre) for April through June. Logistic parameters predicted from these relationships provided an excellent fit to our measured litterfall data (e.g., Fig. 10).

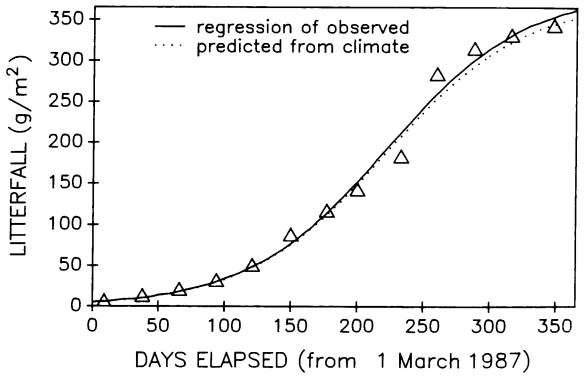

FIG. 10. Observed 1987 cumulative litterfall for control plot 3 (△), and two logistic curves, one fit to the actual data by regression and one with parameters obtained through the regression models (Eqs. 10–12).

Five years of monthly litterfall produce only five points for developing a predictive model, leaving nothing for validation. However, we can use the models to estimate the parameter values and to predict litterfall based on existing climate data (assuming a constant increase in BA from 1989–1990 for illustrative purposes) for April 1989–March 1990 and for April 1990–March 1991. The predicted cumulative litterfall during the first of these 1-yr intervals for the control plots was 3554 ± 397 kg/ha (mean ± SD). This matches well our estimate of 3412 kg/ha as the total amount of old foliage in these stands in March 1989 that should have fallen off during that period, but is substantially lower than the 4526 kg/ha of litterfall measured on the control plots. If the estimated residual (>2-yr-old) foliage mass of 1028 kg/ha is added to the model estimate, there is good agreement. Cumulative litterfall for 1990–1991 is predicted to be slightly higher at 3877 ± 394 kg/ha (not accounting for residual foliage).

These results suggest that we can use this approach over a range of unfertilized stands and climate years, providing us with a tool for assessing the effects of climate change on maximum seasonal LAIs of mature slash pine stands. The phenology functions for litterfall should also be useful in obtaining seasonal LAI patterns (along with needle-elongation measurements or models), with more attention given to the retention of residual old foliage after 12 mo. The usefulness of these relationships must be further evaluated, which will be a straightforward and inexpensive (although slow) process.

Light-use efficiency for slash pine

Biomass increments in young stands, particularly plantations, are highly related to age. After "canopy closure," interannual LAI fluctuations should be low and, as pointed out, are often ignored. Biomass increments for plantations that are nearing rotation age and for most natural mature forests will tend toward zero, with ANPP becoming almost entirely composed of litterfall (and whole-tree mortality in natural stands). Our stands were all still accumulating wood and bark biomass (Table 3c, Fig. 5), with foliage mass fluctuating from year to year (and ANPP highly variable as a result). We have demonstrated that canopy fluctuations may be significant and can be related to climate conditions. However, we cannot yet connect changes in LAI, canopy light penetration and either biomass increment or total annual ANPP for slash pine stands, even when the fertilized plots are included.

This means that "light-use efficiency" may be highly variable from year to year (and seasonally as well). Another interpretation is that these stands are not limited in their annual production by the amount of light reaching foliage for photosynthesis. Our stands produced aboveground biomass of from 1139 to 10 394 $kg \cdot ha^{-1} \cdot yr^{-1}$, or from 5500 to 15 300 $kg \cdot ha^{-1} \cdot yr^{-1}$ ANPP, with an annual rate of 31% PAR penetration through the canopy (69% or 8086 mol/m^2 absorbed by the vegetation). Resulting efficiencies would average 0.05 g total biomass increment per mole of PAR absorbed for control plots and 0.10 for fertilized plots (assuming an average of 4000 $kg \cdot ha^{-1} \cdot yr^{-1}$ for all stands in 1986–1987 and for control stands in 1987–1989, and 8100 $kg \cdot ha^{-1} \cdot yr^{-1}$ for fertilized plots in 1987–1989). Corresponding efficiencies for ANPP (using 8300 $kg \cdot ha^{-1} \cdot yr^{-1}$ for control plots and 14 000 $kg \cdot ha^{-1} \cdot yr^{-1}$ for fertilized plots) would average ≈0.10 for control plots and 0.17 for fertilized plots. Converting from moles of PAR (photon flux) to energy units in megajoules requires spectral data or direct comparison, but can be approximated as 1 MJ = 4.6 mole (Landsberg 1986). Our average efficiencies would then be 0.22 and 0.46 g/MJ for the biomass increment of control and fertilized plots, respectively, and 0.46 and 0.80 g/MJ for ANPP.

In plantations of either eucalyptus or radiata pine in Australia and New Zealand, estimated efficiencies for biomass increments may reach 1.5 g/MJ (Linder 1985, Grace et al. 1987). At best, our fertilized stands in 1987–1988 reached ≈0.6 g/MJ of biomass increment. (Efficiencies of agricultural crops are often >3.0; Monteith 1972, Gosse et al. 1986.) Assuming an energy content for primary production of 20 KJ/g (Satoo and Madgwick 1982), slash pine stands apparently convert from ≈0.6% (for control plots) to 1.1% (for fertilized plots) of incident PAR annually, or from 0.9 to 1.5% of that absorbed. This again is below most other vegetation types, but similar to forests in northern Europe (Jarvis 1981). Estimates of the maximum potential rates of forest energy conversion range up to ≈6% of PAR absorbed (Rook 1985).

The relatively low conversion rates of solar energy for slash pine stands can be contrasted with their nutrient-use efficiencies (e.g., ANPP per unit annual nutrient uptake), which are among the highest ever measured for forests (Gholz et al. 1985*a*). With very low nutrient availability and a relatively warm environment the costs to construct and maintain new tissue, in terms of the necessary nutrient uptake and use of carbon for respiration, are extremely high. Low absorption of solar radiation, facilitated by relatively low LAIs and the clumped canopy structure, reduces the amount of energy that needs to be dissipated through both latent (transpiration) and convective (respiration) heat fluxes, and seems to be an important adaptive feature of slash pine on these sites. Relieving the nutrient-uptake restriction leads to much greater energy conversion (almost 1% absorbed PAR for biomass increment). In this case, increased LAI leads to increased canopy carbon gain in spite of increased foliar respiration, perhaps in part because there is not a proportional increase in absorption of incident radiation.

Conclusions

We found that accurate estimates of seasonal LAI were obtained through the use of our primary technique: destructive sampling each year combined with needlefall and needle-elongation measurements. The maximum annual LAI of these "closed canopy" stands varied 20% over the three study years, although the highest value (fall of 1986) still requires verification (perhaps through the analysis of remote sensing imagery from that year). Needle litterfall was used as a retrospective representation of cohort dynamics (of nonfertilized stands), and indicated that this magnitude of variation can be expected due to differences in climate. Seasonality of litterfall could be described by a logistic relationship, with the annual variation in parameters predictable from the environmental conditions of the previous year. This model is presented as a hypothetical representation of an important climate response by these stands. The large fertilizer response also indicates that changes in nutrient availability over time, for example due to increased atmospheric inputs, would be expected to result in increased LAI and ANPP. This places a premium on the future development of a nutrient-response submodel.

Our attempts to use light penetration through the canopies to predict LAI produced mixed results. Much of the problem apparently results from the highly aggregated (clumped) canopy structure of slash pine trees and stands, which makes light penetration relatively insensitive to changes in leaf area. These canopies did not strictly meet the criteria for application of Beer-Lambert type models of light extinction, indicating more sophisticated models accounting for canopy structure may need to be developed. The use of direct-beam radiation to assess LAI (the DEMON approach) produced mean values for our stands within 1 SD of measured values, although LAIs of individual plots were not well predicted. We were, however, able to demonstrate for the first time the potential use of correlations of seasonal LAI with remotely sensed data. Both of these indirect techniques may be useful in future studies.

Annual ANPP was not related to annual absorbed PAR for these stands. This is partly due to the inherent insensitivity of light absorption to the structure of the canopies. However, it is also likely that changes in annual production reflect changes in LAI and climate factors from at least the previous year. In plantation stands, biomass increments are also highly dependent on stand age. Therefore, it is clear that models of primary production in these stands must take into account cumulative year-to-year and seasonal changes in LAI due to climate and nutrition effects on the fixation and internal storage of carbon.

Acknowledgments

This work was partially funded by NSF Ecosystem Studies Program Grant No. BSR 8106678. The stands for this research were used with the permission of the Jefferson-Smurfit Company, and power was provided to the site by the Florida Electric Power Coordinating Group. We thank Denise Guerin and David Delgado for field and lab assistance, Kenneth Portier for advice on statistical analyses, and Lim Meng Tsai for assistance with biomass data analysis. David Whitehead provided constructive comments on an earlier draft, and A. R. G. Lang, R. McMurtrie, P. Oker-Blom, and two anonymous reviewers provided very useful feedback on later versions. The remote sensing component of this work was funded by NASA Earth Science and Applications Division, while P. J. Curran was on leave from the University of Sheffield, United Kingdom. During this time he held a Senior NRC Research Associateship at NASA/Ames Research Center, California, under a grant from the NASA Life Sciences Division. Assistance with image processing was generously provided by Jennifer L. Dungan. This is Journal Series Number R-00721 of the Institute of Food and Agricultural Sciences, University of Florida, Gainesville, Florida 32611.

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APPENDIX 1

Characteristics of the study plots in August 1986. Plot 16 was relocated in October 1986. C = control, F = fertilized.

Plot no.	Treatment	Tree density (trees/ha)	Plot basal area* (m^2/ha)	Tree* height (m)		Tree* dbh (cm)	
				Mean	1 SD	Mean	1 SD
1	F	1024	24.2	16.4	1.1	17.8	2.8
2	C	1104	21.3	15.5	1.2	16.7	2.8
3	C	1072	18.6	15.5	1.1	16.7	2.3
4	F	1216	25.5	15.0	1.8	16.7	2.8
5	C	1088	26.4	16.4	1.5	17.8	2.4
6	F	1312	27.5	15.6	1.1	16.7	2.1
7	C	1328	30.4	13.4	1.1	17.8	2.5
8	F	1280	28.7	16.0	1.0	17.6	2.4
9	C	1376	29.5	16.1	1.0	17.3	2.4
10	F	1216	25.5	15.6	0.9	16.8	2.1
11	F	1312	26.6	14.8	1.9	16.6	2.5
12	C	1280	30.2	15.9	1.8	17.4	2.7
13	C	1120	26.6	15.5	1.6	17.6	3.1
14	F	992	23.8	15.8	1.9	18.1	2.3
15	F	1120	23.9	14.1	1.7	17.6	2.9
16	C	1200					

* Codominant trees only.

APPENDIX 2

Amounts, forms, and scheduling of fertilizer applications.

Element	Form	Amount of element added ($kg \cdot ha^{-1} \cdot yr^{-1}$)	
		1987*	1988**
N	Urea	180	180
P	Triple superphosphate	70	70
K	Muriate of potash (KCl)	140	140
Ca	Triple superphosphate	46	46
	Dolomitic limestone	50	50
Mg	Dolomitic limestone	28	28
S	Elemental sulfur	50	50
	Triple superphosphate	2	2
Cu	Fritted "Micromix"	0.6	...
Bo	Fritted "Micromix"	0.6	...
Fe	Fritted "Micromix"	1.6	...
Mn	Fritted "Micromix"	1.5	...
Zn	Fritted "Micromix"	1.4	...
Mo	Fritted "Micromix"	0.014	...

* Split into four equal applications on 19 February, 8 June, 18 August, and 17 December.

** Split into two equal applications on 15 March and 15 August.